THE UNIVERSITY OF ALBERTA

POPULATION DYNAMICS, DENNING AND MOVEMENTS OF STRIPED SKUNKS IN CENTRAL ALBERTA

by

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A THESIS

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ABSTRACT

Population dynamics, denning habits and movements of striped skunks were studied on a 130 square kilometer study area in central Alberta from 1971-1974. Numbers of skunks on the study area were greater in 1973 than 1974. Litters were relatively large following the short mild winter of 1972-1973 and relatively small following the long cold winter of 1973-1974. The sex ratio for neonates was not different from 1:1, that of juveniles after weaning favored males and that of adults favored females. Human-related activities accounted for the majority of documented deaths.

Buildings were used intensively for denning. During winter many skunks denned communally; each group consisted of several adult and or juvenile females and one adult male. Males not denning with groups of females during winter denned alone. Skunks remained in winter dens for a minimum of 140 days during winter 1973-1974 and lost a mean of 40 percent of their body weight. Adults travelled relatively short distances from their summer range to or from communal dens; the opposite was true for some juveniles.

Adult males moved greater straight-line distances between captures than adult females. Juveniles moved greater distances than adults and some juveniles moved extensive distances during dispersal. Dispersal occurred from time of weaning (mid-July) until onset of winter denning (approximately November). Direction of dispersal was not random; juveniles travelled towards the gently rolling farmland to the east and south as opposed to the hummocky, more heavily treed area to the north and west.

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Dr. F. S. Chute, Dr. P. Harding, and Mr. A. C. Doell of the Department of Electrical Engineering, University of Alberta, developed the radiotelemetry system. I thank my wife Linda for continued encouragement during the preparation of this manuscript.

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INTRODUCTION

The "bambi syndrome", made famous by Disney type portrayals of many animals, certainly applies to the striped skunk *Mephitis mephitis* (Schreber, 1776). It is one of the first animals recognized by children, because of its presentation as a shy yet friendly animal with unique coloration and "nauseous spray". However, this "picture" of the skunk in the popular sense is in contrast to the significance of skunks in the technical, public health field.

The skunk has had considerable impact in the field of public health due to its involvement in the transmission of rabies and leptospirosis (Ferris and Andrews 1966, Schnurrenburger *et al.* 1970, Sikes 1970). Approximately 50 percent of all documented rabies cases in the United States since 1961 have occurred in the striped skunk (Anon. 1974) and infection is common in skunks of Canada (Webster *et al.* 1970). Skunks accounted for 66 percent of 247 rabies cases in Saskatchewan between 1963 and 1968 (Hayles and Dryden 1970) while 19 cases of rabies in skunks were documented for Alberta from 1970-1974 (Gunson pers. comm.).

Despite the importance of striped skunks in the transmission of rabies and other disease agents, and the relative abundance of this well known host throughout much of populated North America, few ecological studies have been conducted on this animal. Verts (1967) reviewed the literature up to that time and dealt with several aspects of striped skunk biology. Houseknecht (1969), Storm (1972), Sunquist (1974), and Mutch and Aleksiuk (1977) examined several aspects of denning and movements of striped skunks. However, they

revealed little about the overall dynamics of winter denning and dispersal of juveniles, areas of interest to the present author.

Given this background, and the lack of published information on striped skunks in western Canada, the present study was initiated. Hypotheses to be tested included 1) winter weather factors are important to the production and survival of juvenile skunks born the following spring; 2) buildings are important to striped skunks for denning; 3) winter dens are located within or near the summer range of the juvenile and adult skunks which utilize these dens; and 4) distances travelled by independent juveniles during late summer and fall are not greater than distances travelled by adults during the same period. The hypotheses were tested within the framework of the following general objectives: to investigate population dynamics of the striped skunk of central Alberta, its denning habits, and its yearly and seasonal movements, with special emphasis on dispersal of juveniles.

MATERIALS AND METHODS

TERMS

Although accepted terms are used whenever possible, it is desirable to initially define some terms, particularly those dealing with denning and season. (Others will be presented when first used.) During the winter period (November-March) skunks were in or near the winter den. These dens were of two types, including communal dens and dens used by single males. Communal dens were occupied by two or more skunks (and may contain many females but only one male) while single males, those not in communal dens, denned alone. During the summer period (April-October) skunks were absent from the winter den most of the time. Major activities of skunks during the summer period included parturition and lactation in adult females (May-June), onset of dispersal of juveniles and increased foraging for adult females (July-August), and preparation for winter denning in all cohorts (September-October). The cohorts include adult males and females and juvenile males and females.

CAPTURE PROCEDURES

Skunks were captured by live-trapping, night-lighting, and excavation of dens.

Trapping

Skunks were captured by live-trapping from March through November. From April through October, live-traps were placed throughout the study area at locations subjectively determined as good places to capture skunks. During this period about 50 percent of all trap effort was concentrated around buildings; the remaining effort was at fence rows, fringes of woodlots, and culverts. The mean distance from one trap site to the next, from April through October, 1973 and 1974, was 845 meters. During March and November live-traps were placed only near buildings at denning sites. During this period most skunks were in winter dens and most known dens were beneath buildings. Traps, when set, were checked daily. Traps were operated from 1 to 31 days per month dependent upon manpower and work priorities.

Four types of traps were used: wooden and metal box traps, cat and marmot size National traps[1], and round Rudolph Skunkers[2]. Wooden box traps were used most commonly. There was no detectable difference in response to the various trap types. Traps were baited approximately once per week, usually with chicken entrails. During April through October, a few traps were moved from unsuccessful trapping locations to areas where capture was considered probable.

1. Tomahawk Livetrap Company, Tomahawk Wisconsin, U.S.A.
2. ABCO Wire and Metal Products, Hayward California, U.S.A.

Night-lighting

Two aircraft landing lights of 200,000 candle power each, mounted on the roof of a one-half ton truck, were used for capturing skunks by night-lighting.

Night-lighting usually started at dusk and continued for four or five hours; optimal vehicle travelling speed was about 25 kilometers per hour. Roads, ditches, and fields were searched. Night-lighting was conducted only during April, May, September, October, and November, because vegetation hindered observations during summer. When observed, skunks were pursued on foot and were handled similarily to live-trapped skunks (see p. 6).

Excavation of Dens

Excavations were conducted at buildings used for natal dens during 1973 and 1974 and at winter dens during December, 1974. The following combinations of techniques were utilized to ensure that all skunks were counted or captured under a building: removal of the building's side or floor boards, raising the building by jacking, and digging below the foundation. Skunks captured in this manner were handled similarily to those live-trapped (see p. 6). There was no indication that capture by excavation harmed skunks. Six juveniles captured on June 25, 1973, appeared healthy at recapture on July 18, 1973.

Skunks located in winter dens in December, 1974 were killed by carbon monoxide while still in the den, as field work on the study area was being permanently terminated then. Skunks were removed after

excavation of the den.

HANDLING AND MARKING PROCEDURES

Live skunks were handled according to the techniques of Jacobson *et al.* (1970). These techniques included release of the skunk from the trap, netting, ear tagging while under the net, suspension from vulsellum forceps for weighing, sexing, general examination and release. Night-lighted skunks were captured with a net and treated as described above. Skunks were tagged in each ear with fingerling metal tags[3]. A different series of 100 was used each year.

Skunks killed with carbon monoxide were checked for signs of previous ear tags and tagged with Ketchum metal ear tags[4] (placed around the lower jaw for later identification). Sex and age were noted (see p. 7). Skunks were submitted for necropsy to the Veterinary Services Division of the Alberta Department of Agriculture, Edmonton, Alberta. Reproductive organs and lower jaws were placed in 10 percent formalin. Brains were sent to the Animal Disease Research Institute, Canada Department of Agriculture, Lethbridge, Alberta to test for presence of rabies.

3. National Band and Tag Company, Newport Kentucky, U.S.A.

4. Ketchum Manufacturing, Ottawa, Ontario, Canada.

AGE AND SEX DETERMINATION

Live-captured skunks were classed as juveniles from time of birth (approximately May) until the following January 1; all others were termed adults. Juveniles were distinguished from adults on the basis of body weight and size, nipple size, and general appearance. Typically juvenile females were smaller, lighter, and more slender than adult females. Nipples of juveniles were poorly developed while those of adult females were usually pronounced. Juvenile males were smaller and lighter than adult males and had long slender faces resembling adult females; adult males had broader faces.

Histological preparations of canines supported the usefulness of the above criteria used for ageing. Roots of canine teeth from most skunks killed during December, 1974, were decalcified, sectioned, and stained by Matson's Audiovisual and Microscopic, Milltown, Montana. Age was determined by counting cementum annuli (Casey and Webster 1975). Ages of thirteen skunks classed as juveniles, when live-captured between September and November, 1974 were verified from histological preparations. The ages of the only three adults of known age, collected from this study, were confirmed by counting annuli.

The penis of the male is readily visible, making sexual determination easy.

RADIOTELEMETRY

A telemetry system was developed for this study by staff of the Department of Electrical Engineering, University of Alberta, Edmonton.

Transmitters were similar to those utilized by Brand *et al.* (1975). The receiving system consisted of a non-directional whip antenna mounted on the roof of a one-half ton truck, a portable hand held directional loop antenna, and a portable receiving unit. Locations of animals were determined by triangulation with a loop antenna (Cochran and Lord 1963). Most telemetry readings were taken during daytime.

LABORATORY PROCEDURES

Reproductive tracts were cleared for counting of scars after Orsini (1962). Most scars on the uterus were darkly pigmented although a few were lighter. Only darkly pigmented scars were counted. Verts (1967) considered lighter scars to be from litters previous to those from the dark scars.

ESTIMATES OF SKUNK NUMBERS

An equation, based on known population parameters for 1973 and 1974, was derived to calculate approximate numbers of skunks on the study area for those years. Details are outlined in Appendix I.

MOVEMENTS

Maximum distances between captures (Brant 1962, Martin 1975) were employed to express minimum straight-line range lengths. This measure, as opposed to other measurements, including average distance between

successive captures (Wolfe 1967) and activity radii (Hayne 1949) and others (see review of Sanderson, 1967) was used because it was considered an approximation of actual distances moved between age and sex cohorts.

A simple linear regression revealed a significant relationship ($P<0.05$) between days from first to last capture and greatest distance between capture locations. Thus movements, as presented, are at least partially dependent upon time between total recaptures. This is logical because more time allows an animal to be recaptured at more locations throughout its range. It also accounts for the possibility of shifting ranges. Therefore, movements are presented for specific time periods.

DATA CONTROL

The Alberta Fish and Wildlife Division conducted population studies on the study area during 1971 and 1972. The author conducted the study during 1973 and 1974. Some results from 1971 and 1972 are included in this thesis, particularly in the population dynamics section. Skunks captured from October through December, 1971 were not used in any analysis dependent upon ageing, since several skunks captured in that period were not aged.

STUDY AREA

A 130 square kilometer study area was located about 65 kilometers southeast of Edmonton, Alberta at approximately 53° 23' N and 112° 43' W (Fig. 1). The study area exceeded the limits of Township 50 by .80 kilometers on all sides. One adjacent section of land to the north, which included the town of Tofield was also part of the study area. Gravel roads grid the entire study area. One paved road, Highway 14, traverses the study area near its northern boundary.

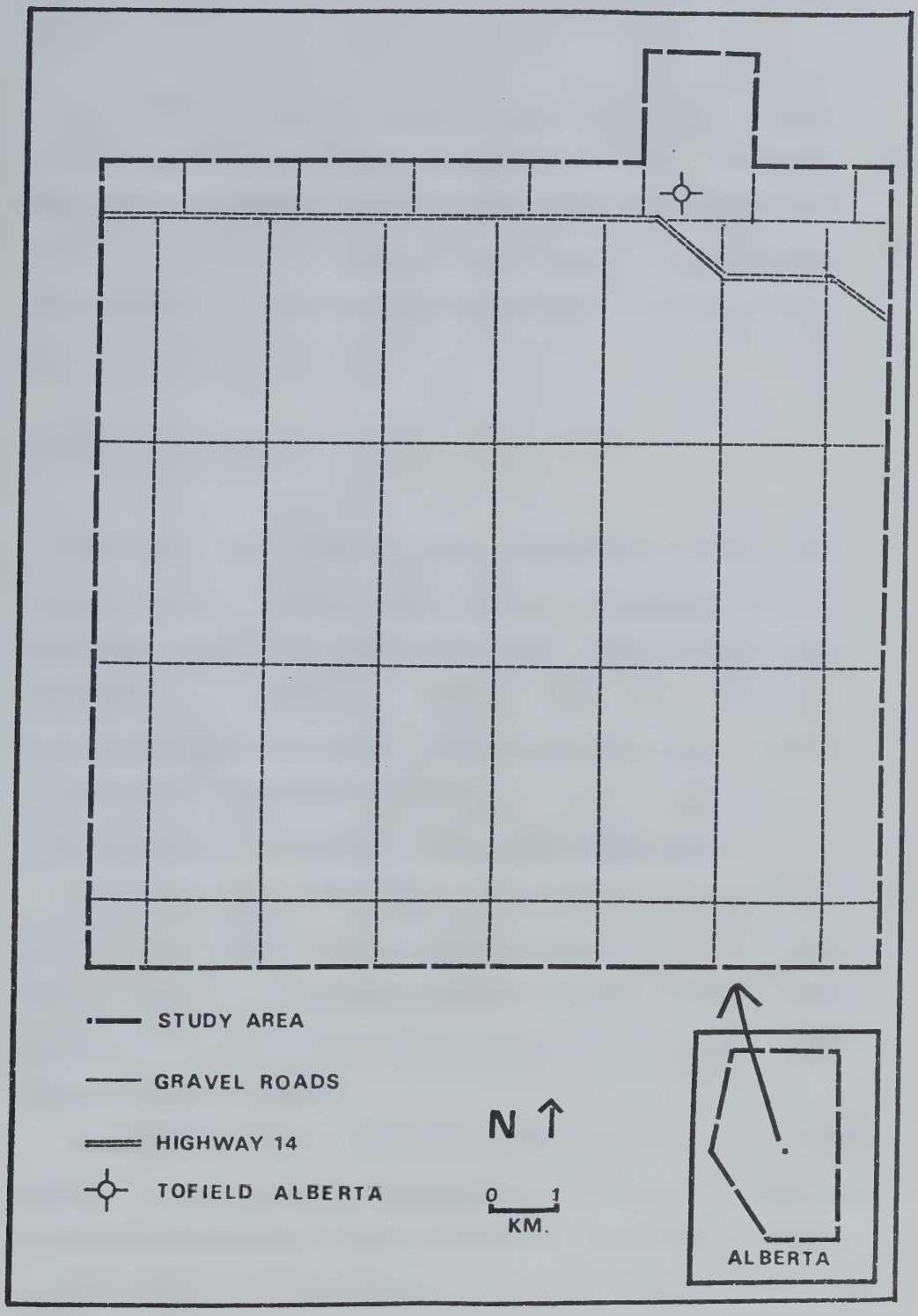
GEOGRAPHY

The study area is a transitional zone between the knob and kettle topography of the Cooking Lake Moraine to the west and north, and the level to gently rolling ground moraine to the south and east (Bayrock 1962). The soils are mostly of the Chernozemic and Solonetzic Orders (Bowser *et al.* 1973) and natural drainage is good.

Approximately 150 small ponds dot the study area. One stream meanders through the northeast portion of the study area. It's influence on skunk movements is likely variable since water levels fluctuate extensively. Several land bridges exist along its course.

About 50 percent of the land is undulating (0-4% slope), 40 percent gently rolling (5-9% slope), and 10 percent rolling (10-15% slope) (Bowser *et al.* 1973). Elevation varies from 785 meters to 701 meters above sea level from west to east.

Fig. 1. Map of the study area showing location of roads, highways, and town-site.


STUDY AREA
GRAVEL ROADS
HIGHWAY 14
TOFIELD ALBERTA
N
0 1
KM.
ALBERTA

CLIMATE

The climate of central Alberta is continental, characterized by warm summers and cold winters (Bowser *et al.* 1973). The mean temperature from May to September is 13°C., and from November to March, -9°C. The frost free period is 100 days. The mean annual precipitation is 40-46 centimeters with about 70 percent falling as rain and 30 percent as snow.

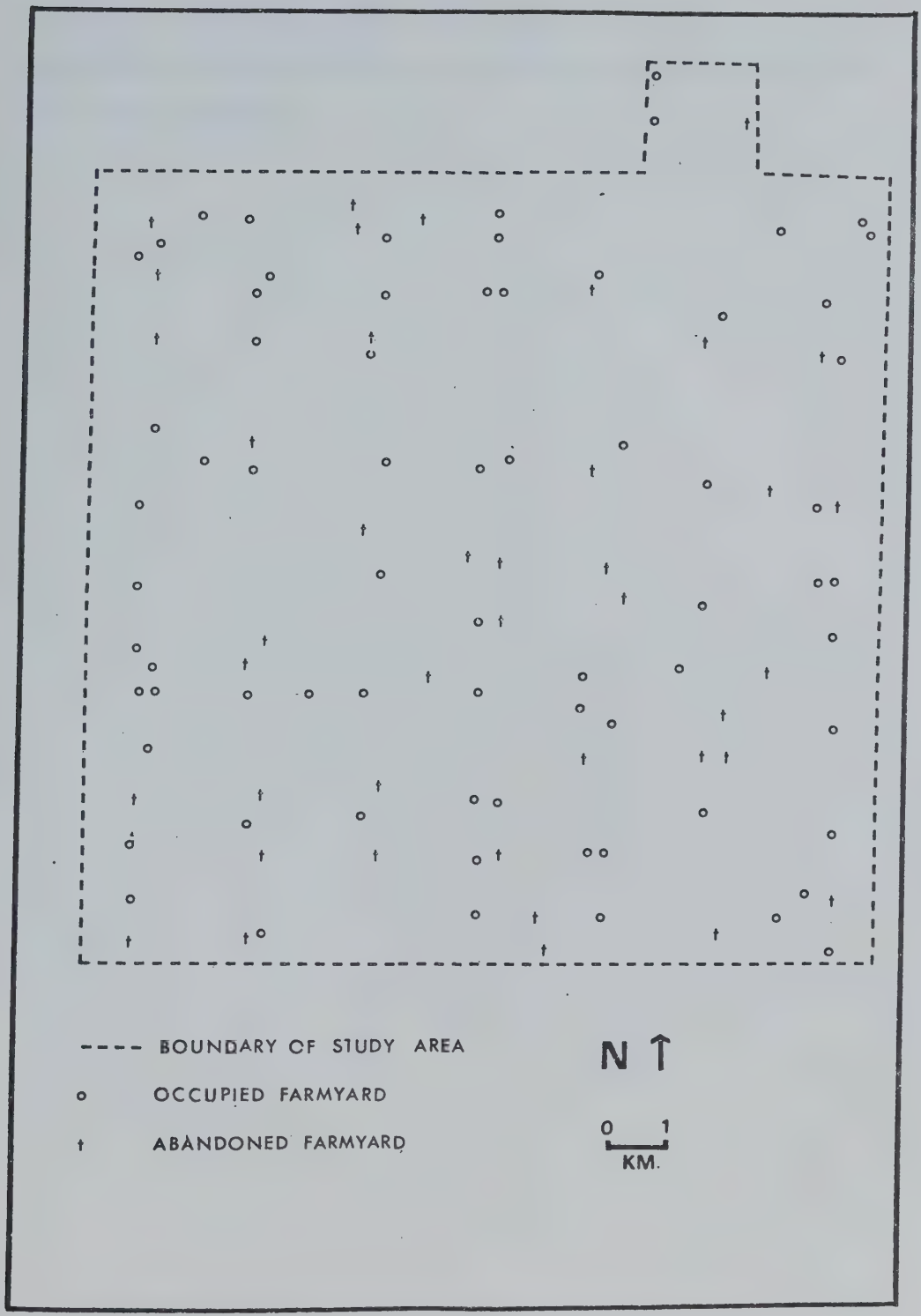
VEGETATION AND LAND USE

The study area is typical aspen parkland (Bird and Bird 1967) which covers much of east-central Alberta. Predominant trees and shrubs are aspen poplar *Populus tremuloides*, balsam poplar *Populus balsamifera*, willow *Salix* spp., saskatoon *Amelanchier alnifolia* and chokecherry *Prunus virginiana*. Brome grass *Bromus* spp. is common in most ditches and abandoned farmyards. Native grasses such as rough fescue *Festuca scabrella* occur in undisturbed areas.

Only the extreme west portion of the study area is not under intensive cultivation. Eight woodlots, ranging from 30-65 hectares exist on the study area; most are near the western boundary. Smaller brush patches are numerous in low or hilly areas, fencerows, road allowances and in farmyards.

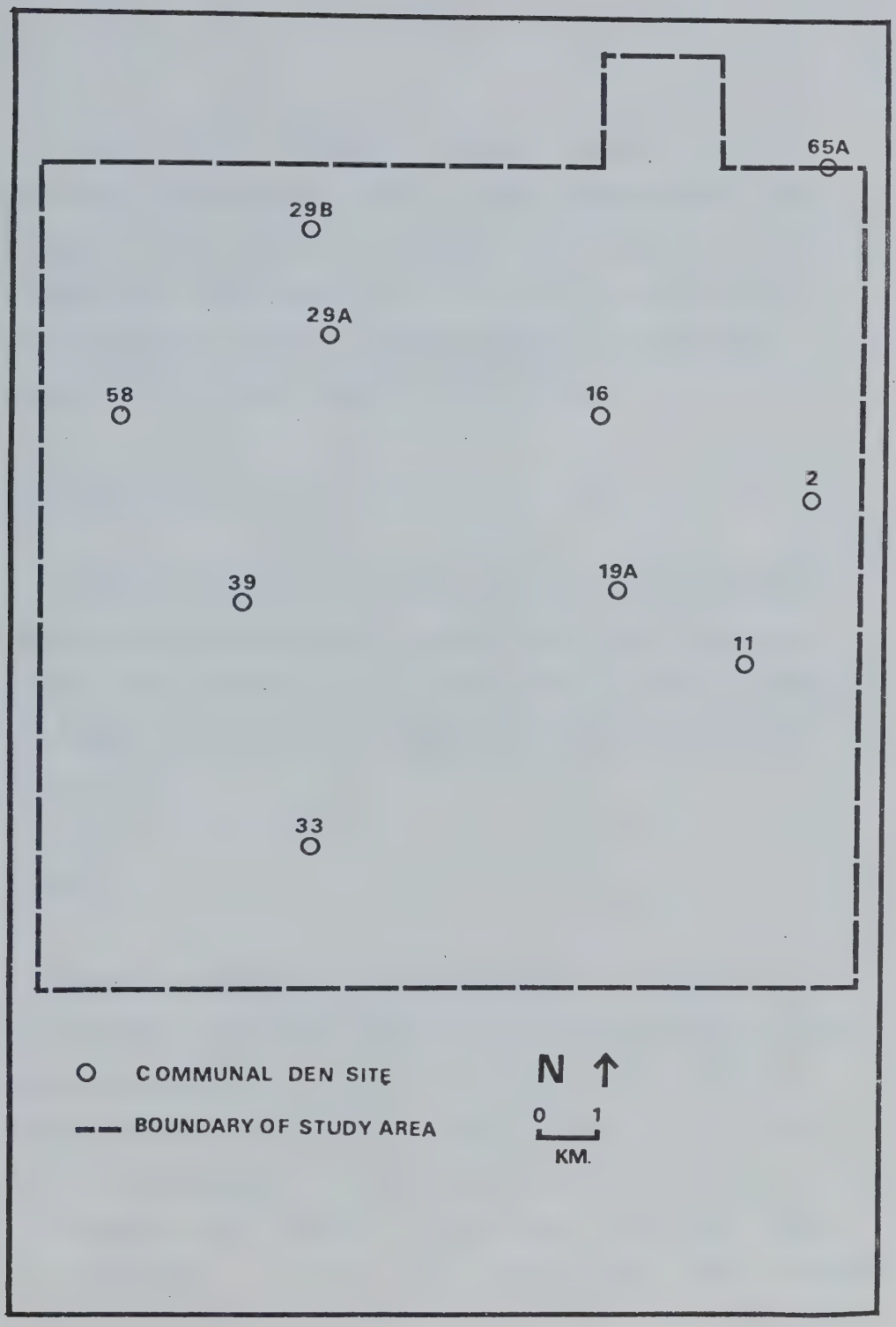
Most farms are about 205 hectares in size; cereal crops, forages, domestic livestock and poultry predominate. A total of 72 farm-sites occupied by man and 40 unoccupied farm-sites was located on the study area (Fig. 2). Some buildings were common den-sites

Fig. 2. Distribution of occupied and abandoned farmyards on the study area.


BOUNDARY OF STUDY AREA
OCCUPIED FARMYARD
ABANDONED FARMYARD
N
0 1
KM.

for skunks. Location and den-site number of ten prominent winter dens (all at building sites) located on the study area from 1971-1974, are shown in Figure 3.

Fig. 3. Ten communal den-sites located on the study area which were used one or more years during 1971-1974.


65A
29B
29A
58
16
2
39
19A
11
33
COMMUNAL DEN SITE
BOUNDARY OF STUDY AREA
N
0
1
KM.

RESULTS

From 1971-1974, 323 striped skunks were captured a total of 876 times by live-trapping (Table 1), night-lighting (Table 2) and excavation of dens (Table 3). Analysis of these captures, radio-telemetry data, and observations in the field, provided the basis for presentation of data on population dynamics, denning, and movements of the striped skunk in central Alberta.

POPULATION DYNAMICS

Population demography data were collected to document baseline information on striped skunks in central Alberta and to determine how the various aspects of the population such as numbers, reproduction, and weights are related to one another and to data on denning and movements.

Numbers

Using the equation presented in Appendix I, an estimated 337 and 126 skunks were on the study area in 1973 and 1974, respectively indicating densities of 2.4 and 1.0 skunks per square kilometer. Despite increased live-trapping and night-lighting effort in 1974 over 1973, approximately 1.6 times more skunks were captured by live-trapping, night-lighting, and excavation of natal dens in 1973 than 1974 (Tables 1, 2, and 3). Thus, there were short-term fluctuations

Table 1. Trap effort and striped skunk captures from live-trapping, 1971-1974.

Year	Months Trapped	Trap-nights	Total Captures	Number Skunks Captured	First[a] Captures
1971	Aug-Nov	2495	118	59	59
1972	Apr-May Aug-Nov	1890	60	46	32
1973	May-Nov	4082	319	98	76
1974	Mar-Nov	4757	218	76	55
Totals		13223	715	279	222

[a] Skunks not captured previously.

Table 2. Summary of results of night-lighting for striped skunks, 1971-1974.

Year	Period night-lighted	Kilometers travelled	Total captures	Kilometers/ capture	First[a] captures
1971	Sep-Oct	853	7	122	4
1972	Apr-May	736	15	49	4
	Sep-Oct	712	7	102	6
1973	Sep-Oct	967	8	121	3
1974	May-Jun	700	5	140	3
	Sep-Oct	924	3	308	3
Totals		4892	45	109	23

[a] Skunks not captured previously.

Table 3. Striped skunks captured by den excavation in 1973 and 1974.

Year	Type of den	Total captures	First[a] captures
1973	Natal	49	48
1974	Natal	18	15
1974[b]	Winter	49	15
Totals		116	78

[a] Skunks not captured previously.

[b] Includes skunks killed by gassing in December, 1974.

in the total numbers of skunks on the study area between 1973 and 1974.

Reproduction

Aspects of reproduction analyzed included month of breeding, percent of adult females breeding and/or raising young, and litter size.

Skunks bred from late February to early April, based on the reproductive condition of females captured and a mean gestation period of 63 days (Verts 1967) (Table 4). Most breeding occurred from late February to mid-March. At least 9 of 10 females whose breeding dates were estimated during spring 1974 were pregnant before leaving the communal den during early April of that year.

There were no differences ($X^2 = 0.13$, $P > 0.05$) in the percent of adult females that raised young in 1973 and 1974. Thirty-two of 35 (91%) adult females captured between May and September, 1973 were either lactating or the nipple size indicated they had raised young that year compared with 10 of 13 (77%) for the same period in 1974. There was, however, a significant difference ($t = 2.55$, $P < 0.05$) in the mean size of litters in 1973 (5.2 of nine litters) and 1974 (2.5 of six litters). These differences were likely partially due to the effects of weather, particularly snowfall and temperature, during critical periods of 1973 and 1974 (Table 5). Snowfall was about twice as great during the winter of 1973-1974 than during the previous winter. Similarily temperatures were significantly colder in November 1973 and March 1974 (the first and last months of winter denning) than during the same months one year earlier. Rainfall from

Table 4. Estimated dates of breeding for female striped skunks, 1972-1974.

Year	n[a]	Date captured	Reproductive condition	Estimated[b] breeding date
1972	7	May 2-11	Pregnant	After March 1-10
1973	10	May 14-30	Not pregnant (Lactating)	Before March 13-29
1974	2[c]	April 25, 28	Pregnant	February 26, March 6
	6[c]	March 26	Pregnant	four by March 1-7, two by March 8-14
	1	May 30	Pregnant (Near Parturition)	After March 27

[a] Females for which reproductive condition was known during March-May, 1972-1974.

[b] Assumes a mean gestation period of 63 days (Verts 1967).

[c] These skunks were killed, others were live-captured.

Table 5. Precipitation and temperatures for the general periods of winter denning (November-March), parturition (May), and lactation (May-June), for striped skunks in central Alberta during 1972-1973 and 1973-1974[a].

Environmental condition	Months	Years 1972-1973	1973-1974	Statistical significance[b]
Days no snow	Sep-Dec	71	61	$P > 0.05$
	Jan-Apr	102	15	$P < 0.001$
Total snowfall (cm)	Oct-Apr	132	267	$P < 0.005$
Rainfall (cm)	Apr-Jun	31.6	15.9	$P < 0.001$
Mean monthly temperatures °C	Oct	3.2	4.3	$P > 0.05$
	Nov	-3.8	-14.1	$P < 0.001$
	Dec	-15.8	-12.9	$P > 0.05$
	Jan	-12.5	-15.3	$P > 0.05$
	Feb	-10.1	-11.1	$P > 0.05$
	Mar	-3.1	-12.1	$P < 0.001$
	Apr	4.2	2.2	$P > 0.05$
	May	11.3	7.9	$P < 0.05$
	Jun	14.4	13.9	$P > 0.05$

[a] Weather records are from Environment Canada.

Snow records are from Edmonton, Alberta, while temperature data are for Camrose, Alberta (a small city about 30 kilometers south of the study area).

[b] Chi-square test used to test for differences in snowfall, "t" test used to test for differences in rainfall.

April-June (when juveniles were still in natal dens) did not appear to be an important factor affecting survival of juveniles as more rain fell during 1973 when litters were largest. However, juvenile survival could have been affected by the significantly colder temperatures during May, 1974.

Age Structure

Age structure was determined for skunks live-captured from August-October, 1971-1974 (Table 6), and from skunks killed during December, 1974 (Table 7). The percent juveniles varied from 49 in 1971 to 70 in 1972 and 1973. Differences in age structure were significant between 1971 and 1973 ($X^2 = 3.9$, $P < 0.05$). There was no significant difference ($X^2 = .72$, $P > 0.05$) in age structure for 60 skunks live-captured during August-October, 1974 and the 45 killed during December, 1974.

Sex Proportions

Sex proportions were determined for adults (Table 8) and juveniles (Table 9) captured from 1971-1974. A total of 37 percent of all adults captured during the study was males ($X^2 = 9.2$, $P < 0.001$). The sex ratio for adults favored females every year, but was significantly different from 1:1 only in 1973.

Approximately equal proportions of juvenile males and females were captured in the natal den prior to dispersal. Fifty-six percent

Table 6. Age structure for striped skunks captured between August and October, 1971-1974.

Year	Skunks captured		Percent Juveniles
	Juveniles	Adults	
1971	18	19	49
1972	23	10	70
1973	52	23	70
1974	35	25	58
Totals	128	77	60

Table 7. Ages of 45 striped skunks gassed in winter dens during December, 1974.

Age (years)	Females	Males	Total
½	16	5	21
1½	7	2	9
2½	8	2	10
3½	4	0	4
4½	0	1	1
Total	35	10	45

Table 8. Sex proportions for adult striped skunks captured between April and October, 1971-1974.

Year	No. skunks captured[a]		Percent males
	male	female	
1971	7	12	37
1972	16	17	48
1973	15	36	29
1974	14	23	38
Total	52	88	37

[a] Repeat captures of same animals not counted.

Table 9. Sex proportions for juvenile striped skunks captured between June and October, 1971-1974.

Year	No. skunks captured[a]		Percent males
	male	female	
1971	11	7	61
1972	15	8	65
1973	28	19[b]	54
	30	26	
1974	7	8[b]	68
	28	13	
Total	84	54	61

[a] Repeat captures of same animals not counted.

[b] Juveniles captured in natal dens; these captures not included in totals.

of 62 juveniles were males ($X^2 = 2.53$, $P > 0.05$). However, significantly more males than females were captured after dispersal from the natal den, but before winter denning (i.e., July-October) ($X^2 = 7.05$, $P < 0.01$) for all years (Table 9). The sex ratio was not different from 1:1 for juveniles captured from July-October, 1973 when populations were high.

Mortality

Human related activity was an important cause of skunk mortality, accounting for 86 of 101 recorded deaths for 1971, 1973, and 1974 (Table 10). Disease, starvation, and other non-human factors, assuming they are present, may be masked by factors considered in Table 10. Sick animals, for example, could easily die in dens or other areas inaccessible for recovery or be at high risk to predation, highway death, etc. Interestingly, 11 skunks were found dead under buildings in 1974, compared to three in 1973 and one in 1971; these skunks died of unknown causes. The increase in death from natural causes recorded in 1974 may have been partially responsible for the decrease in skunk numbers during that year.

Results of radiotelemetry provided further information on skunk mortality. One radio-collared adult female was shot and a juvenile male was hit by a vehicle, while one adult female died of unknown causes and a juvenile male was killed in an open field by an unknown animal.

Table 10. Mortality factors for striped skunks during 1971, 1973, and 1974.

Mortality factor	Years		
	1971[a]	1973[b]	1974[b]
Shot	20	18	2
Hit by: vehicle	5	6	2
or farm machine	3	0	1
Dogs	2	16	2
Poison	4	0	0
Found dead under building	1	3	11
Fell into man-made pit	0	0	5
Totals	35	43	23

[a] Data resulting from a questionnaire sent to all farmers on the study area.

[b] Data collected as a result of interviews with farmers, inspections of dens, and a radio-telemetry study in 1974.

Weights

Some variations in monthly weights between years were evident (Table 11). These were most pronounced for juvenile males and adult females, particularly between 1973 and 1974. Skunks were generally heavier in 1974 than in 1973.

DENNING

Striped skunks in central Alberta are near the northern boundary of their geographic distribution. These skunks are obviously under different environmental pressures than their southern counterparts. Various aspects of the den and denning may, therefore, differ from north to south and from locale to locale. In an attempt to better define the inter-relationships between skunks and their reliance on the den and to document the type of den used in central Alberta, several aspects of denning were investigated. These included communal denning, winter denning by single males, weight lost during winter denning, natal denning, and general aspects of den use.

Communal Denning

Description - In this study all known communal dens were located under abandoned buildings(Table 12). Most buildings used as communal dens had wood or cement foundations with one or two openings; most openings varied from 20 to 35 cm. in height and width. Openings were either man made or had been dug by skunks or other animals. Skunks

Table 11. Mean weight for striped skunks weighed between April and December, 1971-1974. Vertical lines connect means which are statistically significant at the .05 level as determined by Duncan's Multiple Range Test.

Cohort	Year	Weight in Kilograms								
		APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Adult male	1971					5.22±.15[a] (5)[b]	6.31±.170 (4)			
	1972	3.88±.236 (7)	3.87±.310 (5)			4.27 (1)	6.25±1.12 (3)	6.10 (1)		
	1973			4.68±.310 (7)	5.72±.680 (5)	5.72±.680 (5)	5.95±.390 (6)			
	1974			4.89±.720 (4)	6.59±.320 (2)	5.91±.713 (4)	6.25±.636 (5)		6.10±.930 (3)	6.05±.580 (5)
Adult female	1971					3.27±.246 (8)	4.18±.139 (5)			
	1972	1.94±.264 (6)	3.44±.240 (8)			3.02±.520 (2)	3.69±.229 (3)	3.52 (1)		
	1973		2.68±.137 (10)	2.37±.094 (17)	2.57±.135 (12)	3.21±.227 (11)	3.29±.109 (5)	2.72 (1)		
	1974			3.25±.412 (4)	3.46±.350 (5)	3.88±.313 (5)	3.97±.213 (8)	4.0±.160 (7)	3.75±.795 (2)	3.47±.159 (20)

Continued .....

[a] Mean ± one standard error of the mean.

[b] Sample size.

Table 11. Continued.

Cohorts	Year	Weight in Kilograms								
		APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Juvenile male	1971					1.81±.290 (6)	3.31±.400 (7)			
	1972					2.45±.135 (8)	2.69±.194 (8)	2.84±.113 (2)		
	1973			.504±.20 (27)	1.04±.152 (6)	1.93±.108 (18)	2.74±.131 (16)	3.27±.41 (3)		
	1974			.900±.102 (6)	1.34±.219 (6)	3.12±.168 (6)	3.83±.145 (14)	4.18±.178 (12)	4.50±.300 (3)	5.63±.536 (6)
Juvenile females	1971					2.13±.09 (2)	2.90±.210 (8)			
	1972					1.77 (1)	2.14±.231 (5)	2.75±.159 (2)		
	1973			.513±.03 (19)	1.18±.08 (3)	1.61±.135 (12)	2.18±.191 (7)	3.04±.188		
	1974			.790±.08 (9)	.818 (1)	2.09±.180 (2)	2.44±.21 (5)	3.09±.236 (6)		2.65±.094 (17)

Table 12. Important structural aspects of communal dens used by striped skunks and distances from communal dens to the nearest human habitation, 1971-1974.[a]

Den location[b]	Building size (meters)	Openings to den number - size (cm)[c]	Distance to human habitation (meters)
AFH	4.6x7.6	2 30x30;30x30	135
AFH	6.1x6.1	1 25x25	410
AFH	4.6x6.1	2 15x15;15x45	92
AFH	4.6x6.1	2 25x25;25x40	100
AFH	7.6x7.6	3 25x25;25x35;35x35	805
AFH	4.6x7.6	2 30x30[d]	961
AFH	7.6x7.6	2 20x20;30x30	366
AFH	6.1x7.6	3 25x30;30x30;30x30	641
AFH	4.6x7.6	1 20x20	503
AFH	4.6x6.1	1 25x25	1190
AB	4.6x7.6	1 25x25	275
G	3.7x4.9	1 15x30	320

[a] Includes data from two dens slightly outside the study area.

[b] AFH Under abandoned farm house.
AB Under abandoned building.
G Under granary.

[c] Measurements recorded, height to width.

[d] One end of the building was open.

utilized the space between the floor of the building and the soil for denning. The height of this area was approximately 20 to 30 cm. Vegetation (readily available grass species) was pulled into the den and placed in one or two locations apparently for bedding and/or insulation.

Number, Sex and Age of Skunks in Communal Dens - Reports on the numbers and sex ratio of skunks in communal dens are few and the results variable (Seton 1926, Allen 1939, Allen and Shapton 1942). Numbers of skunk per den vary from 2 (Allen and Shapton 1942) to 21 (Seton 1926) and from a male to female sex ratio of 0:2 (Allen 1939) to 1:20 (Seton 1926). In the present study, seven communal dens yielded an average of 6.4 (range 4-8) skunks, with a mean male to female ratio of 1:6.3 (Table 13). Ages of female skunks varied from nearly all juveniles to almost all adults. All males were adults.

Denning Habits - The denning patterns of striped skunks on the study area were variable during the four-year study. Communal dens used in one year often were not used the next (Table 14). In fact, only one of the ten known communal dens was used during every year of the study. Changing patterns of den use were also demonstrated for individual skunks. Six of nine skunks were captured at different communal dens in each of two successive winters.

Despite shifting of communal den sites between years, there was some evidence of stability in this system, since some skunks denned together during different winters regardless of location. Two adult females and one male, and three females which occupied sites 29A and

Table 13. Sex, ages, and numbers of striped skunks captured in seven communal dens in 1974.

Site No.	Numbers				
	Adults		Juveniles		Total
	Males	Females	Males	Females	
29A	1	3	0	1	5
16	1	6	0	1	8
33	1	3	0	3	7
11	1	1	0	6	8
39	0	2	0	2	4
A	1	2	0	2	5
D	1	6	0	1	8
Mean	0.85	3.3	0.0	2.3	6.4

Table 14. Occupational patterns for ten communal dens on the study area that were occupied at least one winter between 1971 and 1974.

Site No.	1971	1972	1973	1974
29A	-[a]	+	+	+
33	+[b]	+	+	+
2	+	+	+	-
58	+	-	-	-
65a	?[c]	+	-	-
11	-	-	-	+
16	-	?	?	+
29B	-	-	-	+
19A	+	-	-	-
39	-	?	?	+

[a] - Den not in use.

[b] + Den in use.

[c] ? Use not determined.

2, (Fig. 3) during the winter period of 1973-1974, used dens 29B and 16, respectively, the following winter. These dens were 1540 and 3650 meters apart.

Skunks in central Alberta began to prepare dens for winter occupancy in late September. At this time in 1973 and 1974 they began to pull grass into future communal dens. Skunk activities had decreased markedly by November at or very near communal dens, about one month after decreased activity elsewhere (Fig. 4).

Data collected via live-capture indicate that onset of winter denning may be different between the age cohorts. Mean distance from the communal den used during the next winter period, was significantly less for adult females than juvenile females during September and October ($t = 2.55$, d.f. = 27, $P < 0.05$) (Table 15), suggesting that adult females occupy communal dens earlier than juvenile females.

A survey of dens containing skunks was conducted during the winter period 1971-1972 to investigate skunk activities throughout that period (Table 16). Ten occupied dens were checked for skunk sign approximately three times per month from early December, 1971 to late March, 1972. No movements were noted beyond a few meters of the den from December through mid-February. A marked increase of activity was evident at six sites by February 18, with tracks leading away from or to the den in four instances. By mid-March movements of skunks away from the dens were common.

Exact dates of final departure from communal dens in spring, 1974 were determined for six adult females captured and radio-collared in March at the den where they had spent the winter.

Fig. 4. A comparison of captures per 1000 trap-nights for striped skunks captured at communal dens and all other trap-sites.

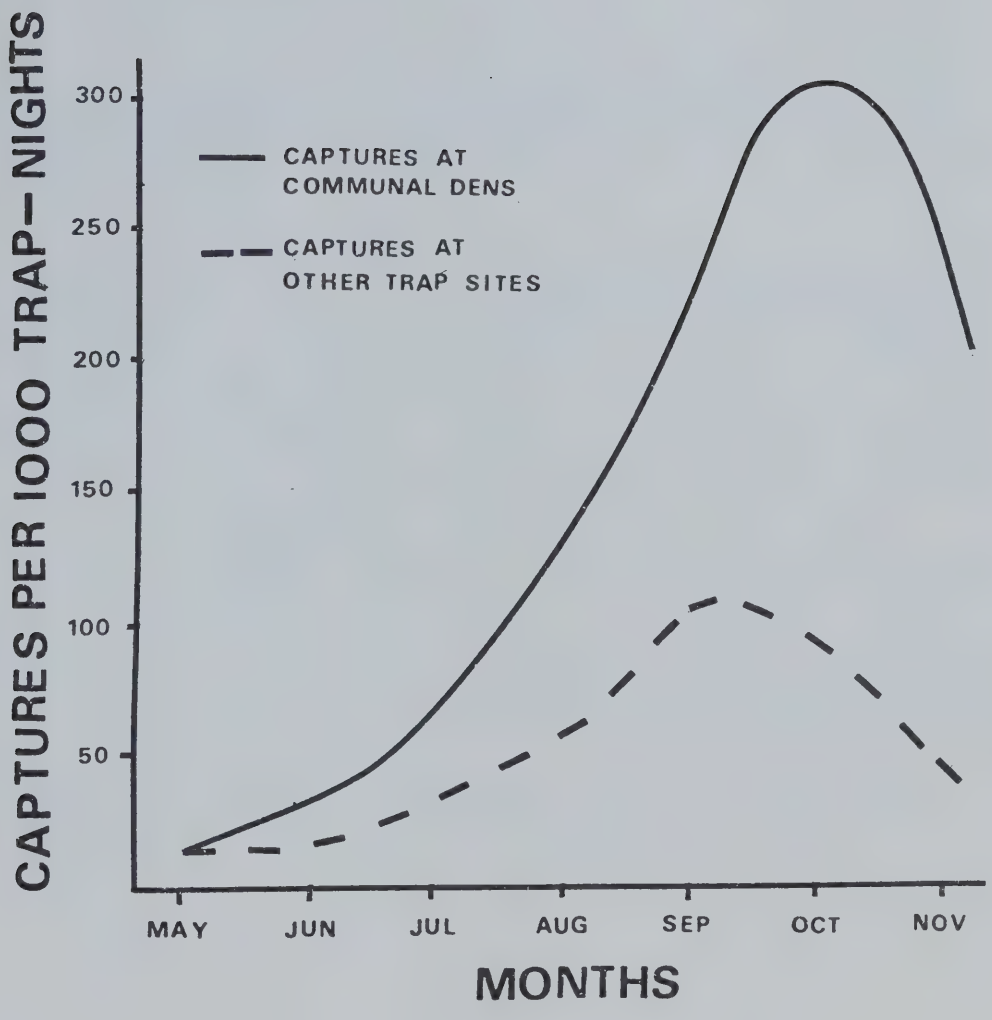

CAPTURES PER 1000 TRAP-NIGHTS
300
250
200
150
100
50
CAPTURES AT COMMUNAL DENS
CAPTURES AT OTHER TRAP SITES
MAY
JUN
JUL
AUG
SEP
OCT
NOV
MONTHS

Table 15. Mean distance from the communal den used by striped skunks during three periods between May and October, before and after communal denning in 1973 and 1974.

Type of Movement	Cohort	Mean Distance From Communal Den[a]					
		n	Apr-Jun	n	Jul-Aug	n	Sep-Oct
To communal den	Adult male	1	2268	5	1287±428	5	1444±277
	Adult female	5	1216±153	9	2179±289	14	1081±231
	Juvenile male	0		0		0	
	Juvenile female	0		3	1341±516	15	2371±429
From communal den	Adult male	1	804	1	1470	2	1212
	Adult female	6	1603±500	2	2093±405	10	1475±392

[a] Mean ± one standard error of the mean.

Table 16.[a] Activities of striped skunks at dens during winter, 1971-1972[a].

Site no.	Den location	Skunk Activity											
		December				January				February		March		
		1	2	3	4	1	2	3	4	1	2	1	2	3
1	Building	[b]											A	B
2[c]	Building										A		A	B
13	Building										B			B
15	Building										B		C	B B
26	Building												B	B
33[c]	Building										A		B	
19a[c]	Building	A		A			A	A			A B		B	B
58[c]	Building												B	
33c	Ground										C		B	B B
19b	Ground													C

[a] Thirteen checks, at approximately eight day intervals, were made throughout the winter; numbers indicate weeks of the month.

[b] Blanks indicate no fresh sign since last check.
A Tracks confined to immediate vicinity of den.
B Tracks leading away from den.
C Burrow through snow and tracks leading away.

[c] Communal dens, others are dens occupied by single males.

Five of six had been captured, but not radio-collared, at the same communal dens the previous November. A total of 29 day-time telemetry readings indicated that these skunks did not occupy other dens from the time of radio-collaring until leaving the communal den between April 2 and 9. The six radio-equipped females spent at least 140 days in the communal den. For this calculation, November 10, 1973 was used as the first day of communal denning, since a 25 cm. snowfall on that date resulted in a complete termination of skunk activities over the entire study area.

Males probably left the winter dens sooner than females although data are scant. Four of four skunks of known sex that travelled over the study area from mid-February to mid-March, 1972 and 1974 were males.

Movements to and from the Communal Den - Prior to this study it was not known how far adult skunks moved to or from the winter den. In the present study these movements were computed as the greatest distances moved to and from the communal den from May-October; that is before and after communal denning (Table 17). Mean greatest distance moved to or from the communal den for adults was 2358 ± 340 meters (range, 240 - 3960 meters). Four adult females, monitored a mean of 69 days after leaving the communal den in spring, 1974 moved a mean greatest distance of 2489 ± 487 meters (range, 1605 - 3330 meters). The distances moved to and from the communal dens are similar to estimated home range lengths (greatest distance between captures) during the summer period (see Table 22). This suggests that adult skunks choose winter dens within or near to their "summer period" ranges.

Table 17. Mean greatest movements to and from the communal den, for striped skunks captured May-October 1973 and 1974, before and/or after communal denning.

Type of movement	Cohort	n	Mean greatest distance ± s.e.[a] (meters)	Range (meters)
To communal den	Adult male	5	2568±300	1649-3342
	Adult female	15	2344±283	240-3784
	Juvenile male	2	2512±643	2051-3338
	Juvenile female	16	2665±400	320-5918
From communal dens	Adult male	3	1649±335	460-3960
	Adult female	15	2046±345	380-3960
Mean	All cohorts	56	2340±402	240-5918

[a] s.e. = one standard error of the mean.

Adult skunks tended to occupy the same general areas during the summer period after communal denning as they utilized the summer period before. Activity centers were calculated according to Hayne (1949) for ten skunks captured at communal dens and also captured during the summer periods before and after communal denning (Fig. 5).

Winter Denning by Single Males

The winter dens of seven males not in communal dens, were examined by excavation during December, 1974. All denned alone and under buildings. Buildings used for denning by single males were of the type used by adult females for natal denning (see Table 19). Most single males probably use ground burrows since so few males were found under buildings despite extensive searches.

Weight Losses During Winter Denning

Striped skunks do not eat while in the winter den, apparently subsisting only on fat reserves. As a result, weight losses are considerable. In the present study five adults and four juveniles captured before and after winter denning lost a mean of 40 and 41 percent body weight respectively, during the winter of 1973-1974 (Table 18).

Fig. 5. Activity centers for ten striped skunks for the summer period (April-October) before and after communal denning during winter. (The circle indicates a communal den; the other symbols indicate activity centers of individuals before and after communal denning.)

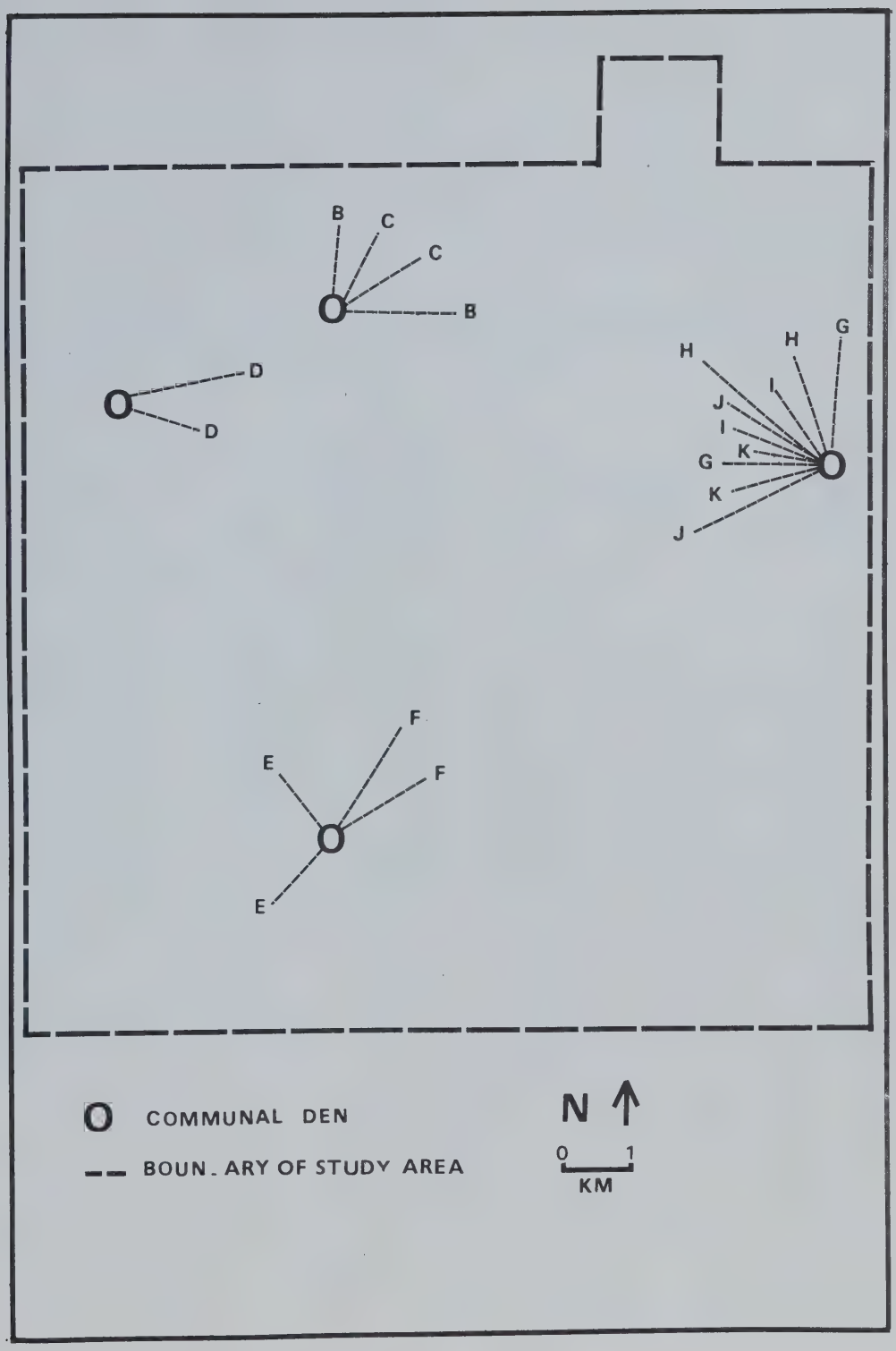

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Table 18. Weight losses for nine skunks captured before and after winter denning during 1973-1974.

Cohort	Fall		Spring		Percent weight loss
	Date	Weight (kg)	Date	Weight (kg)	
Adult male	Oct 31	7.3	Mar 10	4.8	34
Adult male	Sep 17	5.4	Mar 13	3.3	39
Adult female	Sep 20	3.3	Mar 10	1.4	57
Adult female	Sep 20	3.7	Mar 10	2.4	35
Adult female	Aug 21	3.9	Mar 26	2.4	38
Juvenile male	Sep 12	2.2	Mar 12	1.4	36
Juvenile female	Nov 23	2.4	Mar 12	1.5	38
Juvenile female	Oct 30	3.0	Mar 26	1.6	46
Juvenile female	Oct 30	3.4	Apr 1	1.9	44

Natal Denning

Data from two radio-collared females and excavations of dens indicated that the time spent in the natal den was from approximately early May to mid-July, the time from parturition to weaning. During that time females and young may change dens; at least two females moved their young from one den to another. These moves, however, were not substantial in distance. One moved a least nine young 75 meters during late May, 1973 while another moved at least three young 100 meters during early June, 1974. Females also changed natal dens in successive years. Five lactating females captured at natal dens in 1973 used different natal dens the following year.

Twenty-six natal dens were located and described during 1973 and 1974 (Table 19). Of these, 23 were found under buildings and three in burrows. In contrast to buildings used as communal dens (see Table 12), most of these buildings had one or more sides open at the base. Twelve natal dens were located in farmyards occupied by humans. Although three were found in ground burrows, many could have been overlooked.

General Aspects of Den Use

Continual shuffling between a number of dens was typical for striped skunks in summer based on results from radiotelemetry; females with young were an exception. Seven striped skunks (six adult females and one juvenile male) which were fitted with radio-transmitters, occupied a mean of 6.4 dens, used each a mean of 1.5 times, and stayed

Table 19. Important aspects of natal dens used by striped skunks, April-June, 1973 and 1974.

Den location[a]	Size (meters)	Openings (centimeters)	Distance to nearest occupied farmyard (meters)
FG	3.7x3.7	30x30	200
FG	3.0x4.3	46x36	830
FG	3.7x4.3	one-half two side, part of end	0
FG	4.6x6.1	one end	150
FG	3.7x4.3	one side	0
EG	3.0x4.6	two ends	0
EG	4.3x4.9	two sides, part of another	0
EG	3.7x4.9	one end, parts of sides	1550
EG	4.3x4.5	one side	1630
EG	4.3x4.3	two sides	0
EG	3.7x4.6	one end	0
EG	4.6x4.6	one end	0
EG	3.7x4.3	two ends	1540
EG	4.6x4.6	one side	0
AB	2.4x3.0	one end	0
AB	4.3x6.1	two ends, one side	1550
AB	4.0x5.8	most of two sides	220
AB	4.0x5.5	one end	0
AB	3.7x4.6	one side, one end	450
AB	4.5x4.5	one side	330
AFH	4.5x8.5	one end	425
AFH	4.0x6.0	one side	0
T	.90x2.8	one end	0
B			250
B			400
B			1364

a FG Under full granary.
EG Under empty granary.
AB Under abandoned building.
AFH Under abandoned farm house.
T Under water tank.
B In burrow.

at each den for a mean of 2.0 days (Table 20). The seven striped skunks chose buildings over burrows or other natural sites 124 of 146 days ($X^2 = 15.5$, $P < 0.001$) (Table 21).

The potential for contact between skunks and man and/or domestic animals is great. The seven skunks radio-instrumented during the summer period were at or near human occupied yards only 23 percent of 124 days. Since 72 of the 112 farmyards on the study area were occupied by humans, this suggests that skunks avoid denning in human occupied yards to some degree ($X^2 = 36.6$, $P < 0.001$). However in an intensive agricultural area like the study area, skunks can never be far from man or his livestock. For example, three communal dens used most intensively throughout the study were located approximately 100, 100, and 400 meters from human habitations. The mean distance from all other communal dens to human habitations was only 522 ± 100 meters (Table 12). A minimum of 18 skunks was killed by dogs in farmyards on the study area during 1973 and 1974 while domestic cats entered buildings which contained skunks at least five times. Cattle were observed chasing a skunk across an open field in one instance.

MOVEMENTS

The purpose of this section is to compare yearly, seasonal, and daily movements between cohorts, based on results of live-capture and radio telemetry. The data are presented under two major headings: movements of adults and dispersal of juveniles.

Table 20. Number of dens used and consecutive days spent at dens for seven striped skunks fitted with telemetry equipment, April-November, 1974.

Cohort	Days located[a]	Numbers of dens used	Mean times each den used	Mean consecutive days at each den
Adult female	41	7	2.0	2.9
Adult female	19	5	1.0	3.8
Adult female	35	6	2.8	2.1
Adult female	7	5	1.4	1.0
Adult female	8	7	1.1	1.0
Adult female	4	4	1.0	1.0
Juvenile male	32	11	1.4	2.1
Mean	20.9	6.4	1.5	2.0

[a] Does not include skunks in maternal or winter dens.

Table 21. Types of structures used for denning by seven striped skunks fitted with telemetry equipment from April-November, 1974.

Cohort	Buildings		Burrow or woodpile (days)
	Unoccupied[a] (days)	Occupied[b] (days)	
Adult female	34	5	2
Adult female	16	0	3
Adult female	25	6	4
Adult female	0	8	0
Adult female	2	1	4
Adult female	2	2	0
Juvenile male	18	5	9

[a] Does not include skunks in maternal or winter dens.

[b] Unoccupied -- no humans residing at same yard.
Occupied -- humans residing at same yard.

Movements of Adults

Yearly Movements - The mean greatest distance moved in 1973 and 1974 by adults during the live-capture periods of May-October was near 2200 meters (Table 22). Adult males moved a mean greatest distance of 2556 meters compared to 1970 for adult females ($t = 2.04$, d.f. = 46, $P < 0.05$).

Movements determined by live-trapping and radio-telemetry were compared for six adult females monitored by both techniques (Table 23). Mean greatest distance moved was 2804 meters based on results of telemetry and 2760 meters as determined from live-trapping.

Movements Between Years - Skunks ($n = 29$) captured over two years (that is, trapped between May and October of one year, then during the same period the following year) apparently moved only slightly greater distances (Table 24) than those captured within one year (Table 22). The few ($n = 6$) animals captured over three or more years of trapping (Table 24) generally moved greater distances between captures than those captured over one or two years, although one adult female moved very little over four years of trapping.

In spite of the relative stability in movements of adult skunks, some shifting of ranges was documented for adults. An adult male and an adult female each moved greatest distances of more than 5000 meters between 1973 and 1974. Live-capture data indicated no overlap in range between 1973 and 1974, suggesting that shifts in ranges had occurred.

Table 22. Mean greatest distance moved in 1973 or 1974 between captures of male and female striped skunks live-captured between May and October.

Cohort	n	Mean greatest distance ± s.e.[a] (meters)	Range (meters)
Adult male	17	2556±231	1182-4058
Adult female	30	1970±170	700-4216
Totals	47	2197±143	700-4216

[a] s.e. = one standard error of the mean.

Table 23. Greatest distances moved by striped skunks that were radio-collared and live-trapped during 1974.

Cohort	Days monitored by telemetry	Greatest distance between locations by telemetry	Times[a] trapped	Greatest distance between trapping sites
Adult female	93	2522	3 240	2422
Adult female	48	2422	5 262	1615
Adult female	51	2818	2 80	1640
Adult female	100	3664	5 206	3270
Adult female	84	3270	4 247	3664
Adult female	103	3019	16 85	3019
Mean		2804		2760

[a] Times trapped and number of days between first and last capture.

Table 24. Greatest distances moved by adult striped skunks captured during more than one year.

Cohort	n	Years between captures[a]	Mean greatest distance moved ± s.e. (meters)[b]	Range (meters)
Adult male	9	2	2612±637	0-5480
Adult male	1	3	4610	
Adult female	20	2	2276±285	276-5989
Adult female	4	3	3477±691	1970-4728
Adult female	1	4	1970	

[a] Two years = two trapping years.

[b] s.e. = one standard error of the mean

Seasonal Movements - Greatest distances moved between captures during two-month periods, for adults captured during the summer period, were determined (Table 25). The biological importance of these two-month periods to skunks is indicated within the section on terms (p. 3). Adult females moved lesser distances during May-June than July-August ($t = 4.28$, d.f. = 21, $P < 0.001$) and September-October ($t = 2.10$, d.f. = 18, $P < 0.05$). Adult males moved greater distances during September-October than May-June ($t = 2.44$, d.f. = 10, $P < 0.05$). Adult males moved significantly greater distances than adult females during May and June ($t = 3.57$, d.f. = 13, $P < 0.01$) and during September and October ($t = 3.47$, d.f. = 14, $P < 0.01$).

Radiotelemetry data provided information on the movements of adult females prior to and following parturition. Two or more adult females were radio-instrumented during each of the following reproductive periods: pregnancy, lactation, and post-lactation (Table 26). Although sample sizes were small, pregnant skunks (monitored during the period after leaving the communal den but before natal denning) moved distances similar to those of females after lactation. Radiotelemetry data, like those based on live-trapping, indicated that adult females were relatively inactive during the suckling period of May-June. This was followed by periods of more extensive movements during July and August, after weaning of the young.

Daily Movements - Distances between different dens used during consecutive days were recorded for radio-collared skunks as a measure

Table 25. Greatest distances moved during two-month periods for adult striped skunks live-captured between May and October, 1973 and 1974.

Cohort	Mean greatest distances moved ± s.e.[a] (meters)		
	n May-Jun	n Jul-Aug	n Sep-Oct
Adult male	4 1782±234	11 2108±462	8 2849±369
Adult female	11 510±214	12 2207±331	8 1260±269

[a] s.e. = one standard error of the mean.

Table 26. Activity patterns for adult female striped skunks radio-instrumented during different reproductive periods, April-December, 1974.

Reproductive status	Days tracked[a]	Days located[b]	Number dens used	Greatest distance between dens (meters)
Pregnant	Apr 22-May 6	9	3	1771
	May 1 - 15	11	7	3111
	Apr 21-May 1	4	4	3784
Lactating	May 7-Jun 26	43	2	100
	May 17-Jun 12	13	1	0
	Jun 2 - 13	11	1	0
Post lactation	Aug 15-Oct 4	35	6	1647
	Aug 23-Dec 4	57	4	3008

[a] Period radio tracked during specific reproductive period.

[b] Days located by telemetry during specific reproductive period.

of minimum distance travelled in one day (Table 27). Five adult females and two juvenile males moved a mean of 1239 meters between dens used during consecutive days. One adult female moved 2806 meters in one day.

Dispersal of Juveniles

Weaning and Juvenile Independence - Several lines of evidence indicate that juveniles were on their own by late July in both 1973 and 1974. Data used to estimate approximate weaning time were derived from observation of nipple size and shape, results of live-trapping, and radiotelemetry. Nipple size of females which had raised young became markedly smaller and more wrinkled during July. Three of 14 females captured between 15 and 31, July, 1973 and 1974, were lactating compared to 20 of 22 females captured in June, 1973 and 1974.

Two juvenile males from different litters were radio-collared on July 3 and 9 and were absent from their maternal dens by July 16 and 17. The first juveniles were captured in live-traps on July 11, 1973 and July 16, 1974.

Age and Month of Dispersal - For this study a dispersal-type movement is defined as any movement greater than 4800 meters. This distance was chosen because no recaptured adult skunk moved more than 4800 meters during one summer period; in fact none moved more than 4216 meters (Table 22).

Dispersal of juveniles occurred from time of weaning until winter

Table 27. Distance between dens utilized during consecutive days for radio-instrumented striped skunks during March and December, 1974.

Cohort	n[a]	Mean distance moved (meters)	Range (meters)
Adult female	17	1154	245-1852
Adult female	5	877	137-1610
Adult female	10	1278	1006-1771
Adult female	8	2225	1610-2806
Adult female	1	1623	
Juvenile male	3	904	183-2073
Juvenile male	14	615	336-926
Mean	8.3	1239	

[a] Number of times movements between dens utilized during consecutive days were recorded.

denning. Eight of 11 juveniles known to have undergone dispersal, dispersed between the time of weaning and September 1 (Table 28). Some of these juveniles likely continued dispersal after they were last captured. Some dispersal movements of other juveniles were documented during September and October.

Analysis for occurrence of recapture and days between first and last capture during a given trapping year (Table 29) provided an index for time of disappearance (movement or death) from the study area. Juveniles first captured in natal dens during June or during July were recaptured at significantly lower rates than adults captured during June and July, respectively ($X^2 = 15.5$, $P < 0.001$), ($X^2 = 4.1$, $P < 0.05$). Juveniles captured during July and August were recorded on the study area for significantly less time than adults captured during July ($X^2 = 40.5$, $P < 0.001$) and August ($X^2 = 5.5$, $P < 0.05$) respectively. These data suggest that dispersal and/or death of juveniles is extensive during July and August.

Distance and Rate of Travel - Actual distance of dispersal was difficult to determine because of the small study area relative to distances moved by dispersing juveniles. However when juveniles were captured and recaptured on the study area, they moved further ($t = 2.35$, d.f. = 94, $P < 0.05$) than adults ($\bar{X} = 3646 \pm 640$ meters for 48 juveniles captured between May and October, 1973-1974, compared to 2197 ± 143 meters for 47 adults). Four of 62 juveniles first captured at natal dens, before the onset of dispersal, were recaptured within three months and had moved straight-line distances of approximately 4000, 8400, 10,000, and 21,500 meters. One juvenile female live-trapped

Table 28. Sex, dates, distances, and weights for juvenile striped skunks moving more than 4800 meters during 1973 and 1974.

Cohort	Maximum dates between movements	Distance moved (meters)	Weights (kg)	
			initial capture	last capture
Juvenile male	Jul 4-Aug 17	10,120	.7	1.8
Juvenile male	Jun 26-Aug 29	8,372	.7	2.0
Juevnile male	Aug 21-Aug 28	8,052	2.4	
Juvenile male	Jul 24-Aug 14	5,193	2.3	3.3
Juvenile male	Aug 1-Aug 21	4,800	1.5	2.3
Juvenile male	Aug 15-Aug 27	5,086	1.8	1.7
Juvenile male	Aug 28-Aug 30	5,837	1.8	1.6
Juvenile female	Jul 4-Aug 31	21,685	.7	
Juvenile female	Jul 17-Nov 30	13,688	.8	
Juvenile female	Oct 1-Oct 30	5,757	2.8	3.0
Juvenile female	Sep 1 -Oct 22	5,556	2.5	3.1

Table 29. Occurrence of recapture during the same year for adult and juvenile striped skunks captured between May and October, 1973 and 1974.

Month	Age	n	Percent recapture	Mean days first - last capture ± s.e.[a]
May	Adult	16	81	76±16
Jun	Adult	21	62	88±31
	Juvenile[b]	62	8	91±16
Jul	Adult	18	61	71±16
	Juvenile	17	24	19±4
Aug	Adult	13	69	60±14
	Juvenile	31	48	36±8
Sep	Adult	12	75	46±13
	Juvenile	31	52	44±7
Oct	Adult	5	100	44±13
	Juvenile	17	47	29±6

[a] s.e. = one standard error of the mean.

[b] Captured at natal dens.

during early July, travelled 13,700 meters to a communal den that fall. The above figures must be regarded as minimum distances of dispersal since some of these juveniles may have continued dispersal after the last capture.

Limited evidence suggests that juveniles may move extensive distances in a short time during dispersal. Examples include a radio-instrumented juvenile male that moved nearly 8 kilometers in six days; a juvenile male that travelled 5.8 kilometers within a maximum of two days; and a juvenile female that moved 3.7 kilometers in one day.

Proportions Dispersing - Low recapture rates for 62 juveniles first captured in natal dens (Table 29) and the relatively great distances travelled by those recaptured (see above) suggest that many juveniles dispersed from the study area. Juvenile males may be more mobile than young females since twice as many males were captured between July and September, 1971-1974 (see Appendix V and Table 9) and only 9 percent of the juvenile males captured from 1971-1973 were recaptured another year, compared to 33 percent for juvenile females ($X^2 = 8.2$, $P < 0.01$) (Table 30). The possibility that sex specific mortality could also account for the above results cannot be overlooked.

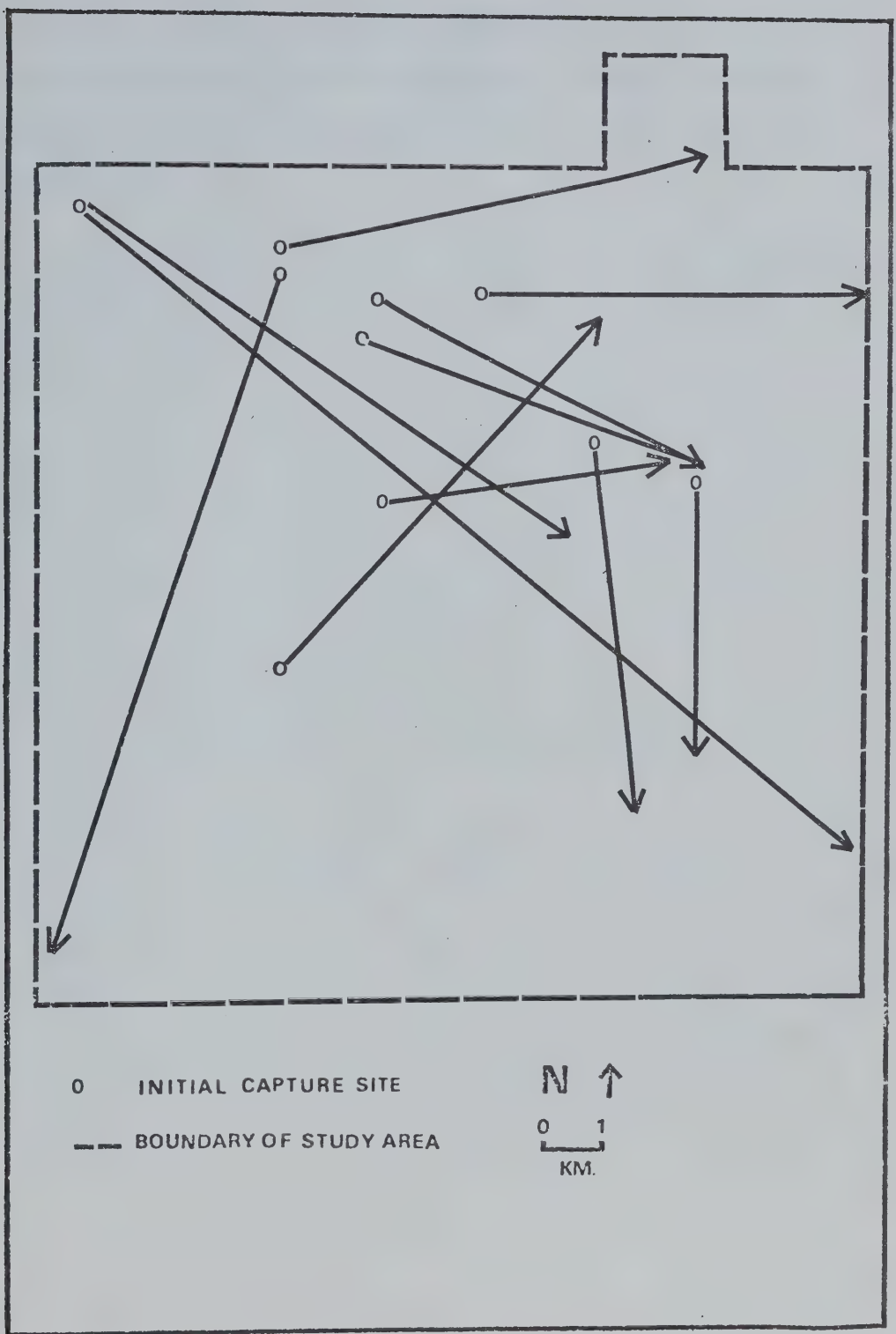
Direction of Dispersal - Directions of dispersal of 11 juveniles moving more than 4800 meters were all away from the northwest (Fig. 6). One skunk moved 13,700 meters southwest; all other moved east and/or south.

Table 30. Recapture rates for striped skunks captured during 1971-1973, and recaptured during another year.

Cohort	n[a]	Percent recaptured another year
Adult male	41	24.4
Adult female	66	33.0
Juvenile male	58	8.6
Juvenile female	49	32.6

[a] Excludes striped skunks captured after October 1 in 1971 and juveniles captured in maternal dens during 1973.

Fig. 6. Direction of dispersal for 11 juvenile striped skunks moving more than 4800 meters.


0 INITIAL CAPTURE SITE
BOUNDARY OF STUDY AREA
N
0 1
KM.

Two littermates captured in a maternal den during 1973 were recaptured later that year after dispersing. Although the distance of dispersal was different, the direction was the same (see double arrow Fig. 6).

DISCUSSION

POPULATION DYNAMICS

Contrasting situations existed within the skunk population on the study area between 1973 and 1974. For example, in 1973 skunks experienced a mild winter (= 1972-1973), high reproduction and survival of young, high numbers of skunks, and low weights for adult females and juveniles during summer and fall. By contrast, in 1974 skunks experienced a long winter (= 1973-1974), low survival of young till weaning, low skunk numbers, and high weights of adult females and juveniles during summer and fall. Based on the nature of these data, it might be possible to predict relative skunk numbers in central Alberta based on the severity of weather conditions during the previous winter. For example:

warm short winter	→	high reproduction and survival	→	high populations	→	low weights
long cold winter	→	low reproduction and survival	→	low populations	→	high weights

If the hypothesis that winter length and severity are influential to skunk populations in Alberta is correct, one would predict high production and survival of young in each of the last three years due to the exceptionally mild winters of 1974-1975, 1975-1976, and 1976-1977. Although no fieldwork has been conducted on the study area since 1974, all evidence from people living on the study area indicates

that skunk numbers were very high during 1975 and 1976. Wynnyk and Schowalter (1976) reported more skunks in the vicinity of the Alberta - Saskatchewan border during September and October of 1975 and 1976, than in similar periods of 1972, 1973, and 1974.

Lower reproduction and survival of young during years of decreased food supply have been documented for several species including wolves *Canis lupus* (Jordan *et al.* 1967), coyotes *Canis latrans* (Clark 1972) and lynx *Lynx canadensis* (Brand *et al.* 1976). This phenomenon likely applies to striped skunks of northern distributions. Striped skunks spend more time within winter dens during long cold winters than mild ones, since the time spent within the winter den is related to winter temperature and snow conditions (Sunquist 1974). The striped skunk doesn't feed in the winter den and, therefore, must rely only on fat reserves (Mutch and Aleksiuk 1977). As a result more reserves would be utilized during long cold winters than mild ones. Breeding occurs from February through the end of March (Wright 1931, Jones 1950, Hamilton 1963, this study), at or near the end of winter denning, when nutritional status of skunks is likely at an annual low. Therefore, it is logical that reproduction and survival of juveniles may be lowered during harsh winters. Downhower and Armitage (1971) documented decreased reproduction in yellow bellied marmots *Marmota flaviventris* following long winters. After long winters, the initiation of the growing season was delayed and the herbivorous marmots were short of food during gestation.

The small litters of skunks in 1974 compared to 1973 probably resulted from mortality of juveniles between late pregnancy and weaning since counts of placental scars for 1974 averaged 2.5 times greater

than counts of juveniles in litters for that year (unpub.). Important causes of mortality would include resorption of embryos and death of juveniles shortly after birth. Verts (1967) found a 13 percent loss of skunk embryos and Rakowski (1972) reported that juvenile skunks weighing less than 29.5 grams died within a few days of birth. Resorption of embryos and the proportion of small, weak, juveniles would be expected to increase in nutritional status of pregnant females was poor. Other possible reasons for smaller litter sizes in 1974 over 1973 would include: weather which might affect juveniles in dens after birth, disease, and predation. Rainfall did not appear to be a negative factor since the size of skunk litters was high when rainfall was high. It is not known if increased rainfall could enhance survival of juveniles in any way. However, relatively cold temperatures during May 1974 may have hampered survival. There was no known difference in disease or predation between years, but the overall importance of these factors to juvenile skunks is largely unknown.

Despite the relatively high reproduction in 1973, fewer adults were located on the study area during 1974 than during the previous year. It seems logical that the same factors responsible for decreased reproduction and/or survival of young during 1974, could account for the decrease of adults during that year compared to 1973. Death from exposure and/or starvation during the severe winter 1973-1974 is probable, particularily since skunks were relatively light in weight during 1973. Sunquist (1974) thought that some deaths of skunks in winter dens in Minnesota, were due to starvation.

Allen (1939) and Allen and Shapton (1942) attributed marked yearly fluctuations in striped skunk populations of Michigan to "disease". However, in the present study, agents of rabies, leptospirosis, and

tularemia, common diseases for striped skunks (Houseknecht 1969), were not found (Appendix II). Some emigration of skunks may have occurred following high skunk numbers in 1973, however it is unlikely that this phenomenon alone could cause the reduction of adults observed on the study area in 1974.

The relationship between winter weather, population density and weights of adult females and juveniles during summer and fall could be explained as follows. During years when litters are smaller (more common after severe winters) female skunks utilize less energy nursing and caring for young than during years when litters are larger (more common after an easy winter). Juveniles with fewer littermates would have less competition for milk during nursing than those in larger litters. Because of these factors skunks would gain weight faster in the years when litters were smaller. It is also possible that food items (in addition to milk for nursing young) could be limited during periods of high populations. Although the striped skunk is highly omnivorous (Hamilton 1936), few comprehensive investigations of the species' food habits have been conducted.

In spite of some yearly variations in population numbers, the density estimates of from .5 - 2.4 per square kilometer for the study area are among the lowest reported in the literature (see summary of the literature Appendix III). Scott and Selko (1939) report densities from 0.4 - 1.4 skunks per square kilometer in Iowa, while Ferris and Andrews (1966) reported from 11.5 - 27.0 skunks per square kilometer in Illinois. Important factors that might contribute to variations in skunk density from one location to another include: availability of food items and denning locations, climate, and land use practices.

The sex ratio for adults captured during this study favored females, a finding not unique for skunk populations (Verts 1967, Bailey 1971, Gunson and Schowalter 1976), although the reverse has been reported (Bennett and Nagel 1937, Hamilton 1937, Jones 1939). A sex ratio favoring females suggests greater mortality for males or differential capture rates for the adult cohorts. Considering that adult males are intolerant of one another (Allen and Shapton, this study), they most often den alone during winter (this study), likely compete with other males for aggregations of females (this study), and travel extensively in early spring in response to "sexual urges" (Allen 1939, Ferris and Andrews 1966), it is probable that males die from starvation, fighting, and accidents more frequently than females. The result of the above factors could be a skewed sex ratio. However, the possibility remains that the sex ratio findings for adults on the study area result from some local circumstance. Perhaps more males than suspected live in habitats not sampled.

The sex ratio for juveniles, after dispersal from the natal den, favored males. This may be due to a sampling bias. There is no evidence, nor reason why mortality, specific for females, would be operative shortly after the onset of dispersal. However, this possibility cannot be overlooked. Alternatively, more extensive dispersal for juvenile males is common for many species (see p. 83). It is possible that juvenile males were more active than juvenile females, were captured more frequently and thus the sex ratio favored males.

DENNING

Striped skunks in central Alberta were relatively inactive during winter, in itself not uncommon for skunks (Selko 1938, Dean 1965, Verts 1967), but they remain in winter dens for a longer period (a minimum of

140 days) than reported previously. Verts (1967) reported that a striped skunk remained in a winter den in Illinois for 87 days, Storm (1972) documented a skunk occupying a winter den for 62 days, while Sunquist (1974) reported that skunks remained in winter dens for a mean of 90 and 115 days during two consecutive winters. The difference in time spent in the winter den between years was attributed to differential snow and temperature conditions. It is reasonable to conclude that at northerly latitudes, which are characterized by harsh weather conditions during the winter period, skunks spend more time in winter dens than skunks located in warmer regions to the south.

The use of buildings for denning by skunks in central Alberta appears more common than documented elsewhere. Allen (1939) reported that buildings were used occasionally for denning during all seasons, but that burrows were the common dens for striped skunks. Storm (1972) reported only limited use of buildings for denning by skunks. Striped skunks in central Alberta may choose buildings over ground burrows because of the following: dryness, permanence, convenience (already constructed and readily available), increased size over natural dens, and possible increased insulation.

Assuming increased insulation of dens located under buildings as opposed to dens in ground burrows, one could postulate that skunks in Alberta lost less weight over winter than skunks in Minnesota (Sunquist 1974), despite the fact that Alberta skunks spent considerably more time in winter dens than reported elsewhere. Skunks in Minnesota lost 49 and 58 percent of their weight during two consecutive winters (Sunquist 1974) while skunks of the present study lost 40 percent. Mean temperatures during December-February (the only months for which Sunquist

presented temperature data) for Alberta in 1973-1974 and Minnesota in 1967-1968 and 1968-1969 were -12.0°C, -11.6°C and -11.5°C respectively, suggesting that temperatures did not contribute to lower weight losses for skunks in Alberta.

Although skunks in central Alberta used buildings intensively for denning, the overall importance of these buildings to skunk populations is not clear. Perhaps skunks utilized buildings because of preference (e.g. permanence, convenience) as opposed to need (e.g. increased insulation).

Questions regarding how the communal groups are formed are not answered in the literature. Verts (1967) considered it improbable that older males defended harems from other males; on two occasions he observed a juvenile male and a female denning together during fall. Allen (1939) stated that it was unknown whether single males found with groups of females were defending them against other males. Several important aspects that should be considered in questioning how the communal group is formed include: i) only one male, usually an adult, is found in winter dens with groups of females, despite a male age bias favoring juveniles (this study), ii) trap records at communal dens indicate that from two to four male skunks were captured at some sites during October, November, and early December (this study), iii) adult males seem not to tolerate one another (Allen and Shapton 1942, this study), iv) females generally tolerate one another - demonstrated by the fact that females den together during winter, and v) males move greater distances than females during fall (this study). Considering these factors, it is probable that the communal group is gathered during fall in one of the following (or combination of both) ways:

a) Females congregate into smaller groups or possibly remain alone during summer and early fall. Males assemble

the commune by gathering females to an appropriate winter denning site and probably fend off other males

b) Female skunks gather into sizable groups at suitable winter denning sites during late summer and fall, and males compete for these aggregations.

Competition among males seems likely although this was not demonstrated. Three males from this study were observed with fresh scars on their ears or face during October and November, suggesting the possibility of intraspecific aggression. Allen and Shapton (1942) also reported what appeared to be scars, possibly resulting from fighting, on a male in October.

Competition among males for females has been demonstrated for other polygamous mammals. Wapiti *Cervus canadensis* (Struhsaker 1967), and some pinnipeds (Bartholemew and Hoel 1953) are two examples where harems are operative and dominant males compete for receptive females. Armitage (1965) showed that during mating in yellow bellied marmots, several females gathered in burrows with one male; how they congregated was not known.

Although striped skunks do not breed in fall, results from this study show that they may breed before leaving the communal den in spring. Therefore, a male's chance of breeding would be greater if the winter was spent with a group of females. Thus competition between male skunks during fall, for groups of females, may be similar to male-male conflicts seen in many mammals at breeding time.

The genetic relationship of groups of skunks denning together during winter is not known. Sunquist (1974) stated that family relationships within groups of skunks he studied, which denned together, were unknown. Results of this study indicate that dispersal of juvenile skunks is extensive during summer and fall, thus it is unlikely that

skunks cohabiting winter dens are related. Further, since breeding occurs in or near the winter den (this study) inbreeding would be limited. This is a commonly cited advantage of dispersal (Howard 1960, Lidicker 1962, Murray 1967).

MOVEMENTS

Distances, as presented, are only approximations of distances actually travelled by skunks. The relationship between live-trap records and home range is largely unknown (Metzgar 1973). Ambrose (1969) compared movements of *Microtus pennsylvanicus* as determined from isotope and live-trapping methods and concluded that the isotope method revealed the true situation more accurately than the live-trapping method.

In this study, distances moved by adult females, when determined by both live-trapping and radiotelemetry, were remarkably similar, thus supporting the usefulness of live-trapping data in estimating movements of skunks. However, both radiotelemetry and live-trapping data were not obtained for the other cohorts and data were collected from both techniques for relatively few animals. A technique often used in estimating home range is to continue obtaining locations during a specified time period, until plotted range size fails to continue increasing (Godfrey 1954, Fitch 1958, Franklin *et al.* 1975). Unfortunately skunks were not live-captured often enough, nor was radiotelemetry used extensively enough to determine home range size by this method. Nevertheless, data on movements as presented for this study, provide a basis for comparing movements of skunks and are an estimate of home range.

More extensive movements for adult males than for adult females are common for many mammal species (Sanderson 1966). Adult striped skunks in central Alberta followed this pattern. Upham (1967) and Storm (1972) also documented greater ranges for male skunks than females, while Houseknecht (1971) reported that home ranges of females were slightly larger than those of males.

The movements of pregnant female skunks is not well documented (Verts 1967). Jones (1950) suggested that the home range of pregnant females was very small and Verts (1967) implied that females nearing parturition probably moved no more than "one quarter mile" from their den, although no evidence was provided to support these statements. Although my sample sizes were small, I found that movements of pregnant females, after leaving the winter den in spring, were typical of movements of females during early fall. They were undoubtedly less active immediately prior to parturition.

Extensive movements of adult females during July and August were associated with increased independence from the juveniles and extensive foraging as revealed by rapid weight gains. Decreasing distances moved from late August through October are likely associated with decreased demand or availability of food resources and onset of winter denning.

Movement patterns for adult males were not as well documented as those of adult females. It is clear that adult males moved greater distances during September and October than other months. Storm (1972) reported increasing activity of adult male skunks during fall while Houseknecht (1971) reported decreasing length of activity radii

for adult skunks from spring to winter. The increase in distance moved by adult males during September and October may be in response to competition for communal occupancy of dens.

The results of the present study, indicating that juveniles (after weaning) move greater distances than adults, with some moving long distances (up to 22 kilometers), are in contrast to some reports in the literature. Juvenile skunks in Illinois moved up to 2200 meters (Verts 1967), while adults moved farther than juveniles in Illinois and Ohio (Storm 1972, Bailey 1971). The results of Upham (1967), who worked on skunks in North Dakota, are in partial agreement with those of the present study. Juveniles there moved slightly greater distances than adults; one juvenile moved nearly 9 kilometers.

It was difficult to predict the actual distance that juvenile skunks moved during dispersal in central Alberta. Part of the problem was the small size of the study area compared to the distance some juveniles travelled. For example, a juvenile travelling through the study area would often be captured only one or two times and the distance between these captures would be a poor measure of dispersal distance. No doubt some juvenile skunks moved farther than 22 kilometers, the maximum distance of dispersal recorded in the present study. However, since few ear tags were recovered from beyond the study area, there was little opportunity to document exact distances.

Greater dispersal for juvenile males than juvenile females has been reported for several species including yellow bellied marmots (Armitage 1973), Richardson ground squirrels *Citellus richardsoni* (Yeaton 1972), and red foxes *Vulpes vulpes* (Storm *et al.* 1976). However, Smith (1975) reported the opposite for juvenile pikas *Ochotona princeps*. Whether or not juvenile skunks in Alberta disperse differentially is not clear.

The preponderance of males captured during July, August, and September, and the fact that more females than males captured as juveniles were later recaptured as adults, may suggest more extensive dispersal for males. However more research is needed to fully explain this aspect of dispersal. For example, no juvenile of either sex born on the study area was known to be present during another year and the two juveniles known to have moved the greatest distance during dispersal were both females.

During 1973, when skunk numbers were high, approximately equal numbers of juvenile males and females were captured from July until October as opposed to a higher proportion of juvenile male skunks captured in other years. Assuming skunks were captured more frequently when they were more active, the above observation may indicate an increased incidence of dispersal among juvenile females during a year of high density. Archer (1970) indicated increased dispersal with greater population densities for some rodents. Presumbaly, some intraspecific process would be triggered by increasing population size, thus causing increased emigration.

Direction of dispersal was not random, with most juveniles moving towards the semi-open gently rolling farmland to the east and avoiding the more heavily treed hummocky land to the west of the study area. Previous investigators have concluded that striped skunks prefer areas of mixed habitat including open areas, bluffs, and ravines (Hamilton 1943, Burt 1948, Schwartz and Schwartz 1959). Verts (1967) reported an inverse correlation between heavily treed areas and skunk captures. General observations of skunk sign indicated an abundance of sign to the east and limited sign to the west of the study area.

Given the above findings I have concluded that skunks in central Alberta prefer habitats similar to those described in the literature and that dispersing juveniles generally moved in the direction of most favorable habitat. This opinion is shared with some workers (e.g. Howard 1960) who suggested dispersal would be directed towards those areas where animals are maximally adapted to survive and populations relatively dense. Others (e.g. Grinnell 1914, Lidicker 1962, Gadgil 1971) who reason that highest densities are found in the most favorable habitats, suggest that dispersal will be directed towards less favorable areas to avoid competition.

Numbers of skunks are greater in the general direction that juveniles dispersed than in other directions from the study area. However, it was not known if densities east of the study area were greater or less than densities on the study area. Although juvenile skunks in this study, dispersed in the general direction of favorable habitat (relatively high skunk densities), perhaps they were forced to occupy poorer habitats within those areas.

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Appendix I. Equation used to estimate numbers of skunks on the study area during 1973 and 1974.

$$N = (Fy \times Fd/Ft \times L) + F + M$$

N = Estimates of skunk numbers after dispersal from the natal den. This estimate is for the year that data are presented in the equation.

(Fy x Fd/Ft x L) = This portion of the equation is used to calculate estimated numbers of juveniles. Fd/Ft is a constant used to estimate the total number of females on the study area.

Fy = Number of captured adult females which raised young. This was determined by the appearance of nipples of adult females captured from May to September.

Fd/Ft = Numbers of adult females killed in communal dens on the study area during December, 1974 divided by those which had been captured earlier that year.

L = Mean number of young in natal dens.

F = Total adult females. This estimate was calculated by multiplying females captured from May through October times Fd/Ft.

M = Total adult males, calculated from the sex ratio for adult skunks captured between May and October.

The above equation is subject to several assumptions:

1) Females captured May through October, 1973 and 1974 and in communal dens during December, 1974 met assumption for capture-recapture calculations (Poole 1974).

2) Tagged to untagged ratios for adult females which were examined in communal dens during December, 1974 were typical of captured to uncaptured ratios for adults during 1973 and 1974.

The validity of assumption #2 is questionable. Females in communal dens during December, 1974, were likely a random sample of females on the study area and captured to uncaptured ratios for skunks on the study area were likely similar between years. However a greater percent

of one cohort may be captured than another; that is, is it valid to calculate adult males from the male to female sex ratio? Verts (1967) thought a greater percentage of males may have been captured than females in the population he studied. If this was the case for adult males in this study, estimated numbers of males would be greater than actual numbers.

Appendix II. Diseases of striped skunks on the study area which were killed by carbon monoxide during December, 1974.

Disease	Number sampled	Number positive	Agency
Rabies	49	0	Animal Disease Research Institute, Lethbridge
Tularemia	49	0	Alberta Veterinary Services Division, Edmonton
Leptospirosis	49	0	Alberta Veterinary Services Division, Edmonton

Appendix III. Estimates of striped skunk population densities recorded in the literature.

Density estimate skunks/kilometer^2	Location	Authority
4.9	Michigan	Allen and Shapton 1942
4.4-4.6	Ohio	Bailey 1971
0.7	Missouri	Bennitt and Nagel 1937
5.4-10.8	Maine	Dean 1965
11.5-27.0	Illinois	Ferris and Andrews 1966
12.0	Pennsylvania	Jones 1939
0.4-1.4	Iowa	Scott and Selko 1939
1.9-3.1	North Dakota	Upham 1967
3.5-14.3	Illinois	Verts 1967
0.5-2.4	Alberta	This study

Appendix IV. Sex proportions by year and month and sample size for each time unit (in parenthesis) for adult striped skunks captured between April-October, 1971-1974.

Month	Captures Males-Females				Percent males (by month)
	1971	1972	1973	1974	
Apr		7-6[a] 7-6[b]			54(13)
May		5-7 5-8	7-10 7-10		40(30)
Jun			1-13 2-18	4-4 4-4	21(28)
Jul			3-9 5-18	1-5 2-5	23(30)
Aug	5-8 5-8	1-0 1-2	3-3 9-12	4-4 4-5	43(46)
Sep	2-4 4-5	3-2 3-3	1-1 7-5	3-7 6-10	44(43)
Oct		0-0 1-1	0-0 1-1	2-3 6-8	39(18)
Percent males (by year)	37(19)	48(33)	29(51)	38(37)	37(140)[c]

[a] First captures for each year.

[b] First capture for each month.

[c] Percent males for all years.

Appendix V. Sex proportions by year and month and sample sizes for each time unit (in parenthesis) for juvenile striped skunks captured between June-October, 1971-1974.

Month	Captues Males-Females				Percent males (by month)
	1971	1972	1973	1974	
Jun			28-19[a]	7-8	
			28-19[b]	7-8	56(62)
Jul			6-5	6-1	
			6-5	6-1	67(18)
Aug	6-2	8-1	13-11	5-2	
	6-2	8-1	18-12	6-2	69(55)
Sep	5-5	5-5	10-6	11-4	
	7-5	8-5	16-7	14-5	67(67)
Oct		2-2	1-4	6-6	
		2-3	4-7	15-9	53(40)
Percent[c] males (by year)	61(18)	65(23)	54(56)	68(41)	60(138)[d]

[a] First captures for each year.

[b] First captures for each month.

[c] Juveniles captured in natal dens (June) not included.

[d] Percent males for all years.